

SOME RECENTLY DISCOVERED SILURIAN FISH REMAINS. A LINK IN THE CHAIN OF ORGANIC EVOLUTION.¹

EVER since the days of Agassiz and Murchison the subject of the Lower Palæozoic Fish Fauna has been the most sensational in the department of Palæichthyology, mainly on account of the existence at that early period of forms known as Cephalaspidian and Pteraspidian (Osteostraci and Heterostraci of recent classifications), so strangely constituted as to be well-nigh irreconcilable with any of our recent and more familiar fishes. Analogy to certain living species (ex. Coffer Fishes) seemed to suggest that, though archaic, these forms are among the most specialised of all known fishes, and while there has been a general consensus of opinion that this may be so, recent tendency has gone to regard them as the specialised

their unique interest. Great though the memoirs of these and other investigators as concerning these strange organisms, none of them, from a point of view of general interest and accuracy of detail, excel those of the author of the two under review, our foremost authority in Palæozoic Ichthyology. His descriptions and restorations of these creatures are everywhere reproduced, and it is matter for sincere congratulation that he should recently have been compelled to return to their study.

Most particularly does the above remark apply to the Pteraspidiæ, with the determination of the systematic position of which the monographs before us are mainly concerned, and the conclusions arrived at are the more welcome, in view of a recent attempt to deduce, from the discovery of supposed resemblances in the minute structure of their plates and the exoskeleton of the King Crabs, a belief in a genetic relationship between the two—one of those notoriously flagrant flights

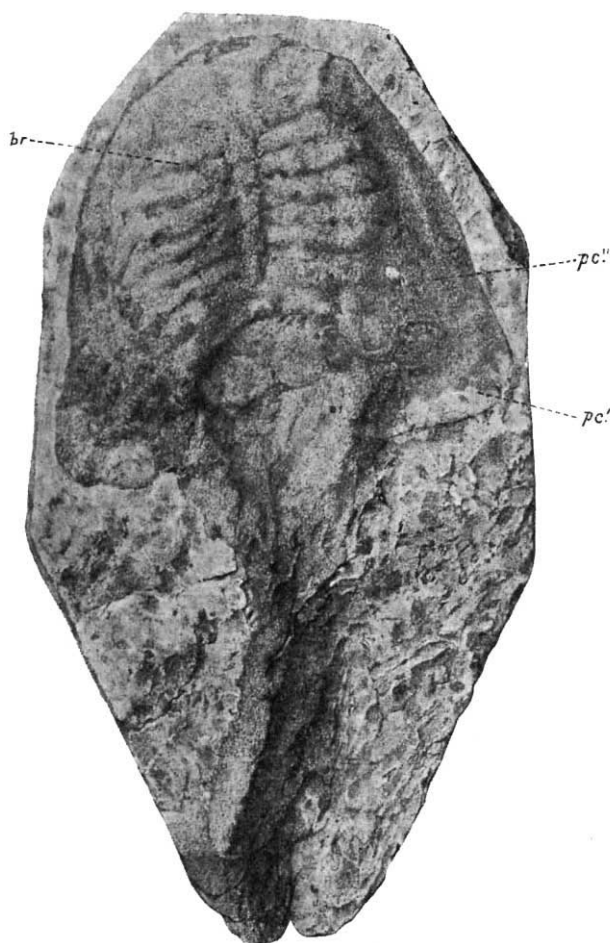


FIG. 1.—*Thelodus Pagei*, dorsal aspect, one-third natural size.

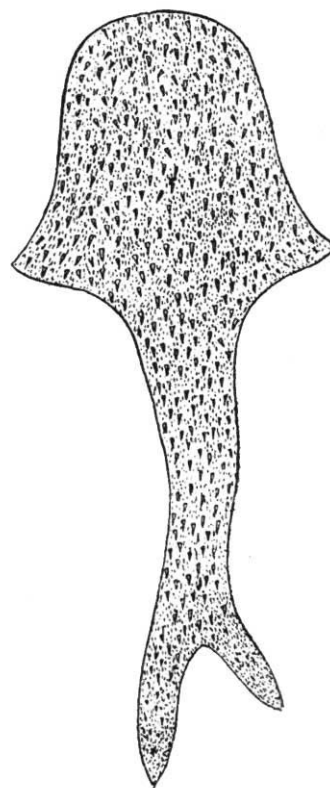


FIG. 2.—*Lanarkia spinosa*, restored outline, with spines, half natural size.

representatives of an ancient and primitive stock, believed by some to have been aqnaous, and even akin to the Lampreys and Hags, which in our modern classificatory systems are not admitted to the Class Pisces at all.

Pander, McCoy and Huxley are among the names of past-masters memorably associated with the record of their early discovery; and, in later years, Powrie, Lankester, Jaekel, Reis and others; while Rohon has quite recently made them the subject of far-reaching generalisation in cephalogenesis, which, though extravagant, has sufficed to maintain

of fancy which during recent years have done so much to bring pure morphology into unjust ridicule. Needless it is to say that the author of the memoirs dismisses this as unfounded.

Conspicuous among Dr. Traquair's later papers on these remarkable forms is that describing (*Proc. Roy. Phil. Soc. Ed.*, vol. xii.) a giant Cephalaspis (*C. magnifica*) from the Old Red Sandstone of Caithness. At the time of its appearance (Dec. 1893) it seemed to those interested to give promise of further unique material from the Scottish Palæozoic; and, sure enough, in his penultimate discourse as Swiney Lecturer, the author, on October 12, 1898, announced at South Kensington the discovery of the remains here under consideration. At that lecture he dealt fully with the long known *Coelolepis* scale, and dissipated the anomalies which had hitherto beset it, showing it to

¹ "On *Thelodus Pagei*, from the Old Red Sandstone of Forfarshire," and "Report on the Fossil Fishes collected by the Geolog. Survey of Scotland in the Silurian Rocks of the South of Scotland." By R. H. Traquair, LL.D., F.R.S., being Nos. 21 and 32 of Part 3, vol. 29, *Trans. R. Soc. Edinb.*

be the shagreen granule of a remarkable fish—shark-like though not a shark; for while possessed of an expanded pectoral and an apparently heterocercal caudal fin, of an extensive branchial apparatus consisting (*br.*) of seven or eight sets of parts, it revealed no trace of teeth, jaws, fin-spines, or pelvic fins; while median fins other than the caudal could not be recognised. The impression created by this announcement was profound, and from the context of his remarks it became evident to the zoologists present that there had been discovered new and probably annectant forms of unique value, and that their best hopes of the Scottish Silurian deposits might yet be realised.

Shortly after his return to Edinburgh, the lecturer produced the first of the two memoirs under review, and therein announced that the fish in question is that described some thirty years ago by Powrie, its discoverer, from the Lower Old Red Sandstone at Turin Hill, near Forfar, by him named *Cephalopterus*, and which he himself, noting that that name was preoccupied, had in 1896 re-named *Turinia*. Further, he announced the very important discovery of its generic identity with Agassiz's *Thelodus*, and, retaining Powrie's specific name, put it finally forward with adequate description and illustration as *Thelodus Pagei*, a member of the family *Cœlolepidæ*, of the nature of whose representatives it enabled us to form the first comprehensive idea.

This discovery of the generic relationship between the so-called *Cephalopterus* and *Thelodus* furnished the keynote to the main series of observations which followed, and the author very properly made the *Thelodus Pagei* the subject of a first special memoir, introductory to the second. Towards the conclusion of this he lays special stress upon the peculiar characters of that which he regards as its pectoral fin-fold, which, according to his description, would appear (Fig. 1, *pc. pc.*) to extend along the branchial free border, and to be "continuous anteriorly with the outline of the head"; while, of its posterior lobe, he remarks that the "lappet-like expansion" which it forms "suggests an analogy with the cornual flaps of *Cephalaspis*, which were originally considered by Lankester as the equivalents of pectoral fins." To this, to our reading the most noteworthy, passage in the whole monograph we shall return. Passing on, the author, pointing out that while the *Cœlolepid* in most respects resembles the *Pteraspidian* its dermal covering points to an *Elasmobranch* affinity, concludes that through the *Thelodus* allies the *Heterostraci* may have had a common origin with the primitive *Elasmobranchs*—an argument previously formulated by Reis, except that he regards the *Pteraspidiæ* as degenerate.

So much for the first memoir, which, if it alone contained all that has come to hand, would have marked an epoch in our knowledge of these most mysterious of fish forms.

Turning now to the second memoir, it may be said that the materials described in it were only obtained in 1897, and that the fact that it was not until the author received and compared these with the Powrie specimen that the identity of that became evident. Hence the delay in the final determination of this. The 1897 collection was obtained by Messrs. Macconochie and Tait while searching the Silurian Rocks of the Lesmahagow district of Lanarkshire, and it was by the latter gentleman supplemented in 1898 by material which included one of the new genera. The total yield has been five genera, of which four are new, and eight new species, and in the earlier part of the monograph the author, retaining the ordinal name *Heterostraci* for the *Cœlolepid* and *Pteraspidian* forms, extends the definition of the former, regarded as a family of the order, so as to include *Thelodus* and the first of his new genera, *Lanarkia* (Fig. 2). Of *Thelodus* two new species (*T. Scoticus* and *T. planus*) are recorded and described, and of *Lanarkia* three species. All are small, and *Lanarkia* is characterised by the presence of a dermal armature consisting of relatively large conical spines, without a basal plate (*cf.* Fig. 2).

For the reception of the remaining three genera, the author has found it necessary to create a new family, the *Birkeniidae*, and a new order, the *Anaspidæ*, setting aside for the moment yet another remarkable form, for which the formation of a new

family of the *Cephalaspidians* or *Osteostraci* has been found necessary. To deal firstly with the *Anaspidæ*, the most remarkable character which the two genera (*Birkenia* and *Lasanius*) possess in common is the possession of a series of median ventral scutes extending along the greater length of the trunk, and bearing each, throughout the posterior series in *Birkenia* (Fig. 3) and their whole extent in *Lasanius* (Fig. 4), a broad compressed spine of formidable aspect. Beyond this very remarkable character they differ *in toto*. *Birkenia*, possessed of a heterocercal caudal fin and a single dorsal, which (*d.*), with its body, is encased in a dense armature of elongated scutes, at first sight suggests, as the author naïvely remarks, a *Palæoniscid* "with the rows of scales running the wrong way!" The characters of its head scutes, the absence of recognisable mouth, of teeth, jaws and operculum, the non-certainty of orbits, however, altogether outweigh these superficial appearances as criteria of affinity, and Dr. Traquair, dealing *en passant* with a series of apertures, which lie along the post-cephalic boundary and which he thinks may be respiratory, with justification makes out a case for an ostracodermatous kinship. *Lasanius* is still more remarkable; since, beyond the row of scutes and the heterocercal tail fin, upon which its presumed affinities with *Birkenia* are based, the specimens by which it is represented agree only in revealing a series of eight post-cephalic skeletal rods, which (*r.*) slope obliquely forwards, and by a forwardly directed series of processes approach their fellows of the opposite side near the dorsal middle line. They are serially disposed behind an oblique chain of ossicles (*r.*'), and

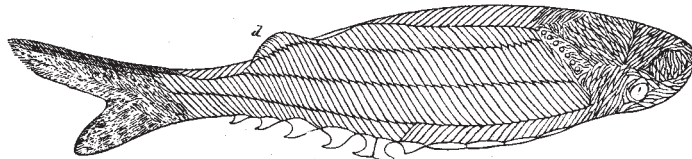


FIG. 3.—*Birkenia elegans*, restored outline, natural size.

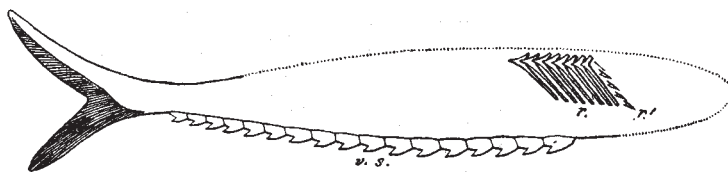


FIG. 4.—*Lasanius problematicus*, restored outline, about natural size.

remarkable in the extreme as are these structures, there is no suggestion forthcoming as to their probable significance. The author points out that *Lasanius* stands "much in the same relation to *Birkenia* as the nearly naked *Phanerosteon* does to the other genera of *Palæoniscidæ*," and we must be content to accept this on his authority, as justification for his provisional association of these strange genera with the *Ostracodermi*, pending further discovery, which can alone help us towards a fuller solution of the problem they present.

The remaining genus described as new is *Ateleaspis*, for which the author also creates a new family of the *Cephalaspidian* order *Osteostraci*. This genus is small, and beset by "shagreen bodies" which on the head have "coalesced into small polygonal plates" that in the tail region unite to form "flat rhombic scales." It is further remarkable for the joint possession of the configuration of a *Thelodus* or *Lanarkia*, and of a couple of crescentic markings on the top of its head which the author is inclined to regard as the "outer margins of a pair of orbits, placed as in *Cephalaspis*" (such as he has failed to detect in any of the other associated genera described in his monograph as new).

Passing on to general questions of classification and final consideration of the inter-relationships of these noteworthy creatures, Dr. Traquair hesitates, to our thinking rightly, to admit the *Pterichthyidæ* members of the Sub-Class *Ostracodermi*, apparently retaining this for the reception of the *Pteraspidian* and *Cephalaspidian* forms and their allies alone. The main outcome of his work is the association of the former with a supposed *Plagiostome* ancestry through the *Cœlolepidæ*, and he is led to find connecting links in the *Drepnaspidae*, upon the *Pteras-*

pidian affinities of which he insisted in 1896. The sole representative of this family, *Drepanaspis*, from the Lower Devonian of Gmünden in West Germany, was only described by Schliüter in 1887. We append a figure of it, from which it will be seen that while in respect to the possession of central (*c.*), lateral (*pl.*) and rostral (*r.*) plates it "points forwards" to the Pteraspidian type, in the possession of tesserae it "points backwards" to the Cœlolepid; and by appeal to the condition of the Psammosteidae, which the author holds to be near related forms, the "stellate tubercles" of which he has already come to regard as "shagreen-granules which have coalesced," he builds up an argument for the origin of the plates of the higher Pteraspidians by fusion of shagreen-granules in linear series.

Having thus with much justification strengthened his conviction that the Pteraspidian fishes have had a common origin with the primitive Elasmobranchs, and that the Cœlolepidæ, Psammosteidae and Drepanaspidae are in order representative of the ascending series which lead up to the Pteraspidians proper, the author returns to the consideration of the Cephal-

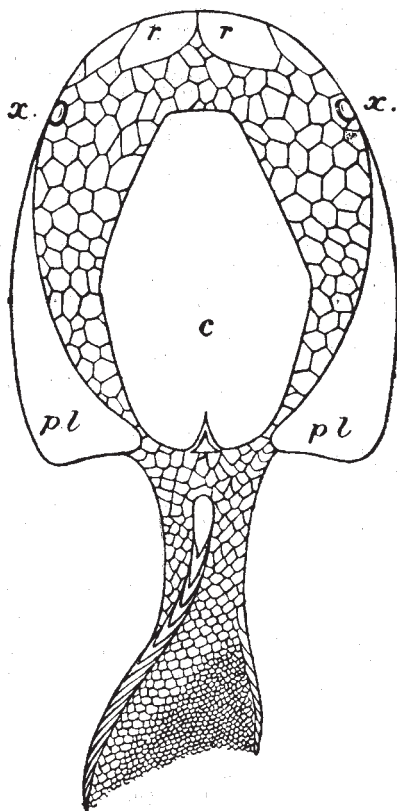


FIG. 5.—*Drepanaspis Gmündenensis*, restored outline, dorsal aspect, omitting surface ornament. *x* = orbit.

aspidians, and, recalling the points of structural community between the aforementioned *Ateleaspis* and the Cœlolepidæ, he concludes that between the Pteraspidian and Cephalaspidian groups there is, "after all, an actual connection."

As might have been expected, he incidentally rejects Claypole's alleged discovery of paired fins in *Palaeaspis*.

It will be remarked that the central point on which the conclusion as to the common origin of the primitive Elasmobranchs and the Ostracodermi (using this term in the author's sense) turns, is the homologising of the plates of the higher Pteraspidians with those of the less fully developed Drepanaspidian and Psammosteid types. So far as the central and rostral elements are concerned well and good; but while admitting the assumed homology of the coronal plate of Pteraspis with the postero-lateral of Drepanaspis, we do not feel so sure about regarding these as the results of encasement of the lateral fin-flaps of *Thelodus* and *Lanarkia*, which are rendered thereby "utterly functionless as fins by being enclosed in unyielding bony plates." In dealing with

these facts, Dr. Traquair has been led into a digression, savouring of leniency towards the lateral fold theory of the origin of the vertebrate limbs, to which indeed he has already expressed himself favourable in his recent memoir on the Selachian *Cladodus Neilsoni*. Following Powrie, he draws attention to the resemblance between the supposed fin-fold of *Thelodus* and that of the living Rays. If in this he is right, the characteristic feature of both is the forward extension into the head-region; and when it is remembered that ontogenetically the pectoral fin bud arises post-branchially, this extension can only be the result of forward rotation, and therefore an index of extreme specialisation. If this be so, the author's implication that "we have here a very interesting point in connection with the much discussed question of the morphology of the paired limbs in vertebrates—a new and important corroboration of the lateral fold theory," can hardly be taken in the sense which would seem intended. There is, however, an alternative reading, to which he has himself pointed the way, which we are most readily inclined to adopt, viz. that already alluded to (*cf. antea*) as involving a comparison between the posterior pectoral lobe of *Thelodus* (*pc.* Fig. 1) and the cornual flap of *Cephalaspis* which, with the author, we believe Lankester to have been right in regarding as "the equivalent of a pectoral fin." To put the case otherwise, we do not see the proof that the presumed forward extension of the fin-fold (*pc.*) is fin-like in structure, and we incline to the conclusion, especially in view of the perforation of its supposed investing plate by the so-called respiratory aperture in *Pteraspis* (1) that it is this alone which has been converted into the cornual plate of that genus and the postero-lateral plate of *Drepanaspis*; (2) that this is in all probability represented by the cornua of the Cephalaspidae, which may therefore well be accessory branchial organs probably enclosing a central passage—"atria," in fact, if not actual opercula! wherefore it would be interesting to ascertain whether they enclose a central canal or passage and are lined by shagreen-granules or tesserae, as might well be if this interpretation is correct. And we further suggest as the natural sequence to this (3) that the posterior lobe of the supposed fin-fold of the Cœlolepidæ (*pc.* Fig. 1) alone represents the pectoral member of the true fishes, and is in turn represented by the cornual flaps of the Cephalaspidae; and (4) that the pectoral member of the Pteraspidians has yet to be sought.

We put forward this view with all reserve, and we submit that while it is not opposed to the facts, it still further justifies the belief in a connection between the Cephalaspidian and Pteraspidian forms which Dr. Traquair has revived. All known facts of morphology justify the conclusion that the paired limbs of the vertebrate have been wholly evolved within that phylum, and there are not a few which suggest that the pectoral and pelvic members have been acquired independently in antero-posterior succession. If so, may not the Cœlolepidæ and Cephalaspidae be now regarded (probably with the Pteraspidae as very distant allies) as the representatives of an apodal stage in evolution, at which the pelvic member had not yet come into existence. Their extreme structural simplicity and entire lack of jaws, teeth, and apparent endoskeleton capable of preservation in the fossil state, are certainly not at variance with this view, and under it the old belief in their extremely specialised nature and their presumed degeneration, towards which even Traquair himself inclines, with that in their affinity with the Marsipobranchs, largely disappears.

The question is one for the palæontologist; and while congratulating the officers of the Geological Survey and the Edinburgh Museum upon the addition to their already matchless collection of these wonderful remains, and the author upon the masterly manner in which, as a true morphologist, and with "soul," he has worked them out, we look to him and his friends in the field to furnish the next link in the chain. The present one is a triumph for all concerned, worthy the author of "The Palæoniscidae" and interpreter of *Palæospondylus*, and as marking progress it is equal to anything achieved in the palæontology of the last two decades.

G. B. H.

UNIVERSITY AND EDUCATIONAL INTELLIGENCE.

OXFORD.—The following are among the lectures announced for the present term:—Prof. Clifton, acoustics; Mr. Walker, physical optics; Mr. Hilton, elementary mechanics and physics; Mr. Baynes, elementary heat and light; Mr. Jervis Smith, dynamo and motor machinery and electrical testing; Prof.